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Title page

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Restricted occupancy and environmental specialization of *Ragala ucuquirana-branca* (Sapotaceae) across the Amazon Basin

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Abstract

Background and aims – Understanding the distribution of Amazonian tree species is hindered by sparse occurrence data and strong environmental heterogeneity. Species with wide geographic ranges but restricted habitat occupancy challenge climate-only explanations of distribution patterns. Here, we investigate the environmental drivers shaping the distribution of *Ragala ucuquirana-branca* (Sapotaceae, Chrysophylloideae), a canopy tree native to the Amazon Basin, to disentangle the roles of environmental filters in constraining its realized distribution.

Material and methods – We compiled and spatially validated 72 occurrence records from verified herbarium specimens and long-term forest monitoring plots collected between 1941 and 2025 across the Amazon Basin. Species distribution models were developed using an ensemble framework that combined multiple algorithms and integrated climatic, atmospheric, edaphic, topographic, and land cover variables. Model performance was evaluated using threshold-independent and threshold-dependent accuracy metrics, and habitat suitability was projected across the Amazon Basin.

Key results – Model performance was consistently high, indicating robust discrimination between suitable and unsuitable environments. Soil-related predictors collectively accounted for the largest share of model importance, exceeding climatic and other environmental variables. Soil pH in water (Phh2o) emerged as the most influential predictor of distribution, followed by atmospheric water vapor pressure (Vapr), minimum temperature of the coldest month (Bio6), and the cation exchange capacity (Cec). Although the species exhibits a broad Extent of Occurrence of approximately 1.48 million km², its Area of Occupancy is highly restricted, revealing a spatially aggregated distribution. Suitable habitats are concentrated in the central and western Amazonia, with strong fragmentation toward the eastern and southern margins of the basin.

Conclusion – Our results demonstrate that the distribution of *R. ucuquirana-branca* is strongly constrained by edaphic conditions and atmospheric stability rather than by broad climatic gradients alone. This decoupling between geographic range size and effective habitat occupancy highlights pronounced ecological specialization and potential vulnerability. More

broadly, the study underscores the importance of incorporating soil and atmospheric filters into assessments of species rarity, distribution, and conservation priorities in hyperdiverse tropical forests.

Keywords

Amazonian tree species, Chrysophylloideae, conservation, edaphic specialization, ensemble forecasting, spatial modeling, species distribution modeling, *terra-firme* forests

INTRODUCTION

The Amazon is the largest drainage basin and harbors one of the most complex and diverse tree floras on Earth (Guayasamin et al. 2024), with the Sapotaceae family standing out as a dominant and ecologically significant component of these forests (ter Steege et al. 2006, 2013). Within this family, *Ragala* Pierre (Chrysophylloideae subfamily) is a small genus that comprises about four species and three subspecies concentrated in the Amazon Basin, but extending to the coastal areas of the Guianas, occurring in lowland *terra-firme* forests (non-flooded forests) on clayish and sandy soils (Pennington 1990; van Roosmalen et al. 2000; Swenson et al. 2023).

Species currently placed in *Ragala* have historically been assigned to *Ecclinusa* Mart., and both genera were at times subsumed within *Chrysophyllum* L. sensu lato (Pennington 1990, 1991). *Ragala* was recently reinstated through phylogenetic analyses based on molecular and morphological data (Swenson et al. 2023). These analyses supported the idea that *Ragala* is a distinct genus from *Ecclinusa* and *Chrysophyllum* sensu lato, forming a cohesive lineage sister to *Ecclinusa*, *Elaeoluma* Baill., and *Nemaluma* Baill. (Faria et al. 2017; Swenson et al. 2023).

Diagnostic characters for *Ragala* include oblique tertiary venation with areolate higher-order venation, pentamerous flowers and fruits with an accrescent calyx—a key feature identified since Pierre (1891)—a glabrous corolla, and the absence of staminodes (Faria et al. 2017; Swenson et al. 2023). Furthermore, wood anatomy studies confirm that *Ragala* possesses distinct structural patterns that separate it from both *Ecclinusa* and *Chrysophyllum* sensu lato (Kukachka 1981).

A notorious member of this genus is *Ragala ucuquirana-branca* (Aubrév. & Pellegr.) W.A.Rodrigues. This canopy tree, which can reach up to 30 m in height and 45 cm in diameter, is characterized by dark brown scaling bark and a reddish-brown slash with abundant sticky milky latex in the field (Pennington 1990, 1991). Taxonomically, it is distinguished from its close relatives, *R. sanguinolenta* Pierre and *R. scalaris* (T.D.Penn.) Swenson, by its densely ferruginous-tomentose indumentum of short, curly trichomes on the young parts and lower leaf surfaces, as well as its villous reddish fruit (Pennington 1990, 1991). Despite its current well-established taxonomic identity, detailed knowledge regarding the environmental drivers of this species remains necessary to fully understand its ecological niche across its documented range in central and northern Amazonian Brazil and southern Venezuela (Pennington 1990).

Species Distribution Models (SDMs) have become indispensable tools for evaluating how broad-scale environmental shifts impact biological diversity (Hao et al. 2019; Zurell et al. 2020). These correlative frameworks function by integrating georeferenced occurrence data with spatially explicit environmental layers, most notably climatic variables (Miller 2010). By quantifying the relationship between a taxon and its habitat, SDMs allow researchers to delineate geographical ranges and forecast shifts in distribution across space and time (Guisan and Zimmermann 2000; Miller 2010), being useful for supporting policy decisions in biodiversity conservation (Araújo and New 2007; Guisan et al. 2013).

Given the increasing pressure on Amazonian ecosystems (Flores et al. 2024), there is an urgent need for precise spatial data to guide management strategies for species conservation. Therefore, this study uses ensemble species distribution modeling to: (1) compile and validate available occurrence records of the *R. ucuquirana-branca*, (2) quantify the primary environmental factors shaping its potential distribution, and (3) produce spatially explicit predictions of its suitable habitat across the Amazon Basin.

MATERIAL AND METHODS

Target taxon

Ragala ucuquirana-branca (Fig. 1) is a canopy tree native to the Amazon Basin, typically occurring in lowland *terra-firme* forests. The species is locally known by several vernacular names, such as “ucuquirana-brava-da-folha-vermelha” (Rodrigues 1974), “balata-brava”, “coquirana-branca”, and “coquirana-rocha” (Pennington 1990; van Roosmalen and Garcia 2000). Its distribution is primarily documented in central and northern Amazonia, extending into southern Venezuela (Pennington 1990). Given its restricted distribution, this species serves as an ideal model for investigating how environmental variables shape the distribution of high-diversity tropical tree families.

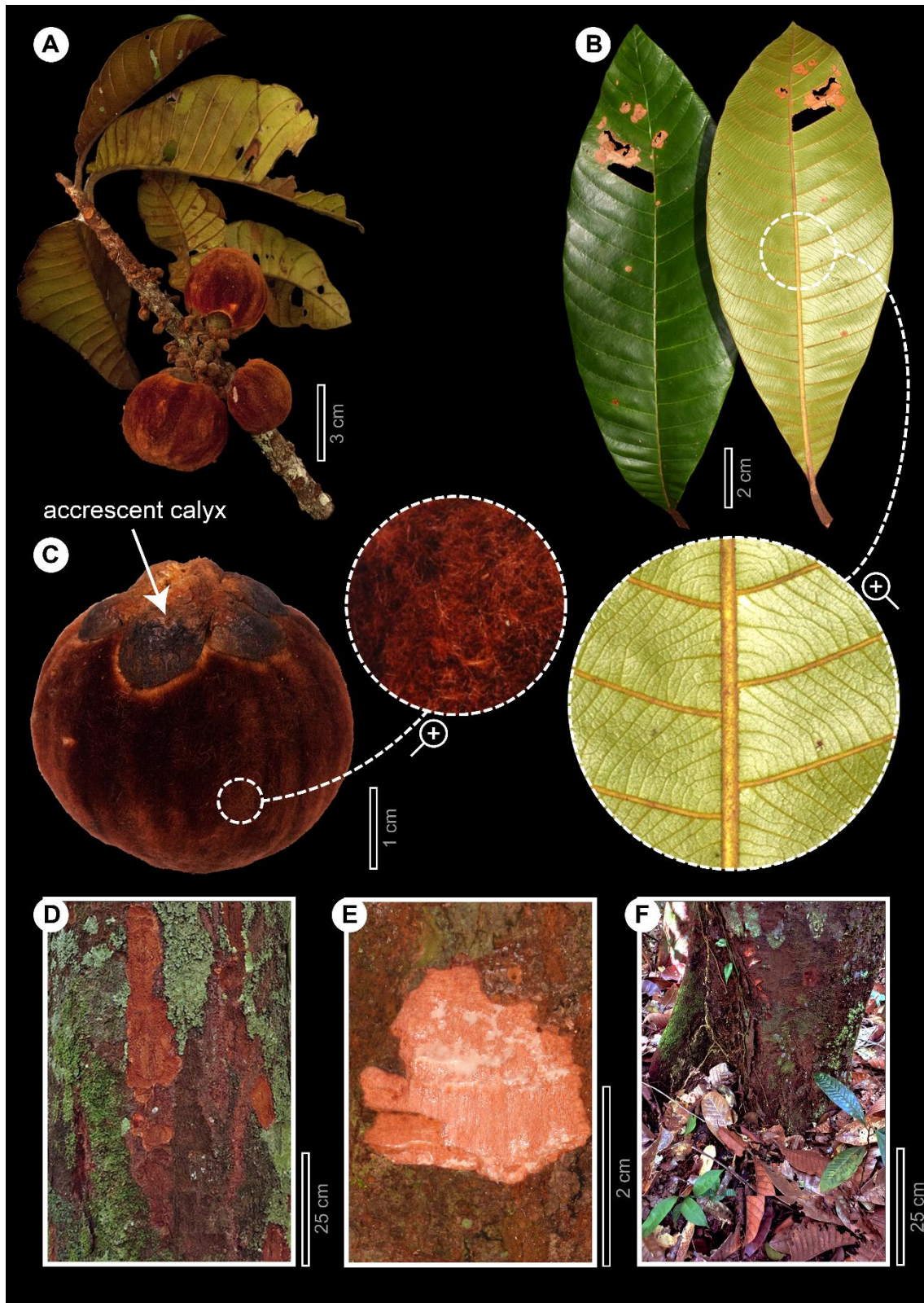


Figure 1. Field images of *Ragala ucuquirana-branca* (Sapotaceae). **A.** Fruiting branch. **B.** View of adaxial (upper) and abaxial (lower) leaf surface, with a close-up of the venation pattern. **C.** Mature fruit with a close-up of the reddish indument. **D.** Bark pattern. **E.** Bark slash showing the milky latex. **F.** Trunk base with small buttresses. Photographs: **A, C** by Isolde Ferraz; **B, D, E** by Francisco Farroñay; and **F** by José Edmilson Souza.

Species occurrence records

We compiled all available occurrence (presence) records from two web-based biodiversity repositories that integrate data from multiple herbaria worldwide: the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>; GBIF.org 2024) and the *speciesLink* network (<http://www.splink.org.br/>; Canhos et al. 2022). In addition, we incorporated records from physical reference collections associated with long-term forest monitoring plots in Central Amazonia, including the *Projeto Dinâmica Biológica de Fragmentos Florestais* (PDBFF) and *Programa de Pesquisa em Biodiversidade* (PPBio). In all cases, only records of preserved specimens were retained. During an initial data screening, we excluded specimens from other genera through taxonomic verification of digital and/or physical specimens, as well as duplicate records (i.e., specimens with the same collector and collection number, even when deposited in different collections).

To minimize georeferencing errors, original coordinates (latitude and longitude in decimal degrees) were manually verified to ensure consistency with the corresponding locality descriptions. When coordinates were missing, they were estimated based on detailed locality descriptions, allowing for reliable georeferencing using the Google Earth platform (<https://earth.google.com/web/>). We also flagged and removed potentially erroneous records by checking proximity to well-known geographic features (e.g., centroids for administrative regions and institutions), identifying spatial outliers, and finding suspicious values or formatting problems using the ‘CoordinateCleaner’ package (Zizka et al. 2019).

In addition to preparing the occurrence dataset for the SDM workflow, we quantified the Extent of Occurrence (EOO) and Area of Occupancy (AOO) using the GEOCAT platform (Bachman et al. 2011). These metrics summarize, respectively, the overall geographic spread and the minimum occupied area represented by the verified records.

Study region

The species’ geographic range was cropped to the extent of the Amazon Basin (sensu Eva et al. 2005), which includes areas of the Cerrado biome and montane regions that drain into the Amazon River. This delimitation of the Amazon Basin (Amazonia sensu latissimo) covers approximately 7,595,000 km² and includes areas of Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname, and French Guiana. All subsequent modeling steps (background selection, pseudo-absence generation, variable extraction, and ensemble forecasting) were performed within this geographic extent to ensure ecological coherence and minimize spatial bias in model performance and properly encompass the full known distributional range of *Ragala ucuquirana-branca*.

Environmental data

Environmental variables were selected to capture the environmental gradients driving the distribution of *Ragala ucuquirana-branca* in the Amazon Basin. The dataset included 37 predictors related to climate, topography, soil, land cover, and habitat heterogeneity (Table 1) that are expected to influence plant physiology, morphology, distribution, and ecology (Toledo et al. 2012; Stein et al. 2014; Lambers and Oliveira 2019).

Table 1. Variables selected for modeling the current potential distribution of *Ragala ucuquirana-branca* (Sapotaceae) in the Amazon Basin. Variables 1–19 are related to climate, 20–22 to atmosphere; 23 to topography; 24–33 to soil; 34–36 to land cover; and 37 to habitat heterogeneity. Data sources: WC – WorldClim 2.1; SG – SoilGrids; and EE – EarthEnv.

N	Label	Description	Unit	Source
1	Bio1	Annual mean temperature	°C	WC
2	Bio2	Mean diurnal range (mean of monthly (max temp - min temp))	°C	WC
3	Bio3	Isothermality (Bio2/Bio7) ($\times 100$)	%	WC
4	Bio4	Temperature seasonality (standard deviation $\times 100$)	°C	WC
5	Bio5	Maximum temperature of warmest month	°C	WC
6	Bio6	Minimum temperature of coldest month	°C	WC
7	Bio7	Temperature annual range (Bio5–Bio6)	°C	WC
8	Bio8	Mean temperature of wettest quarter	°C	WC
9	Bio9	Mean temperature of driest quarter	°C	WC
10	Bio10	Mean temperature of warmest quarter	°C	WC
11	Bio11	Mean temperature of coldest quarter	°C	WC
12	Bio12	Annual precipitation	mm	WC
13	Bio13	Precipitation of wettest month	mm	WC
14	Bio14	Precipitation of driest month	mm	WC
15	Bio15	Precipitation seasonality (coefficient of variation)	fraction	WC
16	Bio16	Precipitation of wettest quarter	mm	WC
17	Bio17	Precipitation of driest quarter	mm	WC
18	Bio18	Precipitation of warmest quarter	mm	WC
19	Bio19	Precipitation of coldest quarter	mm	WC
20	Srad	Annual mean incident solar radiation	$\text{kJ m}^{-2} \text{ day}^{-1}$	WC
21	Wind	Annual mean wind speed (2 m above the ground)	m s^{-1}	WC
22	Vapr	Annual mean water vapor pressure	kPa	WC
23	Elev	Elevation above sea level (from SRTM)	m	WC
24	Bdod	Bulk density of the fine earth fraction	kg dm^{-3}	SG
25	Cec	Cation exchange capacity of the soil	$\text{cmol}(+) \text{ kg}^{-1}$	SG
26	Cfvo	Volume fraction of coarse fragments ($> 2 \text{ mm}$)	%	SG
27	Nitrogen	Total nitrogen (N)	g kg^{-1}	SG

28	Phh2o	pH in water (H ₂ O)	-	SG
29	Sand	Sand (> 0.05 mm) in fine earth	%	SG
30	Silt	Silt (0.002–0.05 mm) in fine earth	%	SG
31	Clay	Clay (< 0.002 mm) in fine earth	%	SG
32	Soc	Soil organic carbon in fine earth	g kg ⁻¹	SG
33	Ocd	Organic carbon density	kg m ⁻³	SG
34	Land2	Consensus land cover - Evergreen broadleaf trees (Class 2)	%	EE
35	Land5	Consensus land cover - Shrubs (Class 5)	%	EE
36	Land8	Consensus land cover - Regularly flooded vegetation (Class 8)	%	EE
37	Shannon	Diversity of Enhanced Vegetation Index (EVI)	-	EE

The near-global standardized environmental layers were downloaded as GeoTIFF raster files from web-based repositories such as WorldClim 2.1 (<https://www.worldclim.org/>; Fick and Hijmans 2017), SoilGrids (<https://isric.org/explore/soilgrids>; Poggio et al. 2021), and EarthEnv (<https://www.earthenv.org/>; Tuanmu and Jetz 2014, 2015) at 30 seconds (~1 km) spatial resolution and under historical (near current) environmental conditions (Table 1). Soil data were downloaded using the ‘geodata’ package (Hijmans et al. 2024a) while other variables were directly from the aforementioned web-based repositories.

To reduce multicollinearity and prevent model overfitting, we selected a subset of weakly correlated bioclimatic predictors (Dormann et al. 2013). Automated variable selection was performed using the *select07()* function implemented in the ‘mecofun’ package (Zurell 2024), which identifies correlated pairs (Spearman’s rank correlation coefficient $|r| > 0.7$) based on environmental values (i.e., the full set of 37 variables) extracted at species occurrence points. Within each correlated pair, we retained the variable with the highest explanatory power, assessed by its univariate importance in a quadratic generalized linear model (GLM) ranked by Akaike Information Criterion (AIC). This procedure resulted in a final set of 21 variables, which were used in all subsequent analyses (Fig. 2).

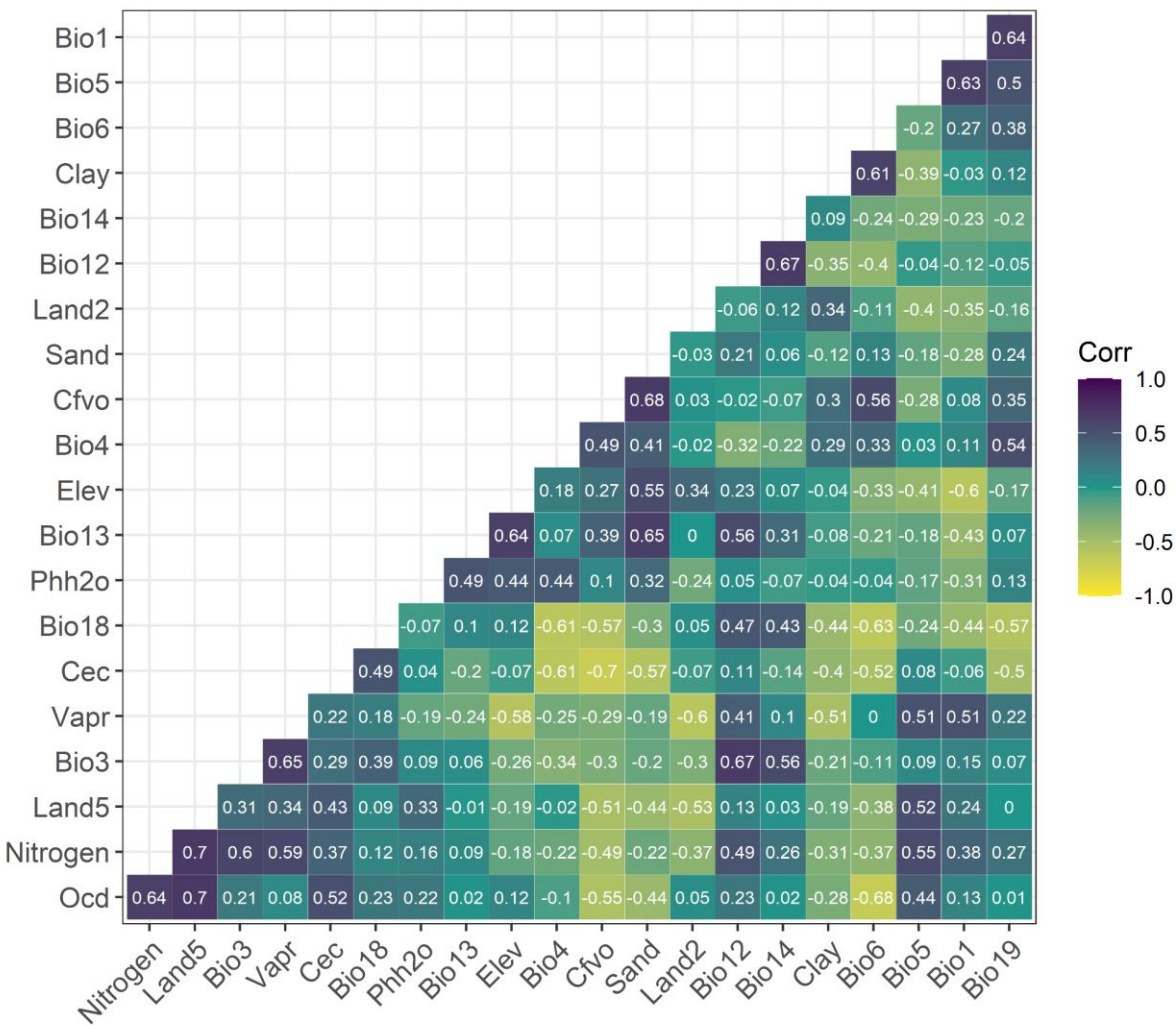


Figure 2. Correlogram plot showing pairwise Spearman's rank correlation between variables selected as predictors ($|r| \leq 0.7$) for further analysis. Darker colors indicate stronger correlations. Dark purple indicates positive and yellow indicates negative correlations.

Ensemble modeling

We modeled species' potential distribution using five algorithms: (1) Boosted Regression Trees (Elith et al. 2008); (2) Classification and Regression Trees (Breiman et al. 1984; De'ath and Fabricius 2000); (3) Generalized Additive Model (Hastie and Tibshirani 1986; Yee and Mitchell 1991); (4) Maximum Entropy (Phillips et al. 2006); and (5) Random Forest (Breiman 2001) (Table 2). We used the 'dismo' package (Hijmans et al. 2024b) to perform Boosted Regression Trees and Maximum Entropy; 'rpart' (Therneau and Atkinson 2023) to perform Classification and Regression Trees; 'mgcv' (Wood 2011) to perform Generalized Additive Model; and 'randomForest' (Liaw and Wiener 2002) for the Random Forest models. We used an ensemble forecasting approach (i.e., combining multiple models for better predictions) to minimize errors (Araújo and New 2007).

Table 2. Summary of the algorithms used in the ensemble species distribution model (SDM). Statistical approach: ML – Machine Learning; R – Regression.

Label	Algorithm	Data type	Approach
BRT	Boosted Regression Trees	Pseudo-absence	ML
CART	Classification and Regression Trees	Pseudo-absence	ML
GAM	Generalized Additive Model	Pseudo-absence	R
MaxEnt	Maximum Entropy	Presence-only (background sample)	ML
RF	Random Forest	Pseudo-absence	ML

We sampled pseudo-absence points across the Amazon Basin. We matched and randomly generated pseudo-absence points, 10 times the number of occurrence points, for all algorithms (Barbet-Massin et al. 2012). Moreover, we randomly split the combined dataset (comprising occurrence records and pseudo-absence data) so that 70% was used for model training and the remaining 30% for testing.

We evaluated the model's performance by calculating the True Skill Statistic (TSS; $[(\text{sensitivity} + \text{specificity}) - 1]$) (Allouche et al. 2006), and the Area Under the Curve (AUC) of receiver operator characteristics (ROC; Fielding and Bell 1997). We generated 10 replications for each algorithm and selected the replicates presenting accuracy values of $\text{AUC} \geq 0.75$ and $\text{TSS} \geq 0.55$ to construct the ensemble rasters. Then, we ensembled the models based on the average of the selected rasters weighted by AUC values ≥ 0.75 (Hao et al. 2020).

To create binary distribution (presence-absence) of the predicted habitat suitability, we applied two threshold-selection methods: minimum (or lowest) training presence (MPT), which consists of the lowest predicted suitability value for an occurrence point; and 10th percentile training presence (P10), which omits all regions with habitat suitability lower than the suitability values for the lowest 10% of occurrence records (Morrow 2019).

All SDM workflow was performed in the open-source statistical software R v.4.4.2 (R Core Team 2024) using custom-made R scripts and add-on libraries. Final maps were prepared using QGIS v3.28.1 (QGIS Development Team 2022).

RESULTS

After data cleaning and spatial verification, a total of 72 unique occurrence records of *Ragala ucuquirana-branca* (Fig. 1) were retained for subsequent analyses (Fig. 3A). These records span collections made between 1941 and 2025 and represent the most comprehensive and spatially vetted dataset currently available for the species. Occurrences are unevenly distributed across the Amazon Basin, with a pronounced concentration in central Amazonia, particularly in lowland *terra-firme* forests of northern Brazil, and a smaller number of records extending into southern Venezuela and southern Colombia (Fig. 3A). In Brazil, records are restricted to the states of Acre, Amazonas, and Pará. No records were confirmed for large portions of the southwestern and southeastern Amazon Basin.

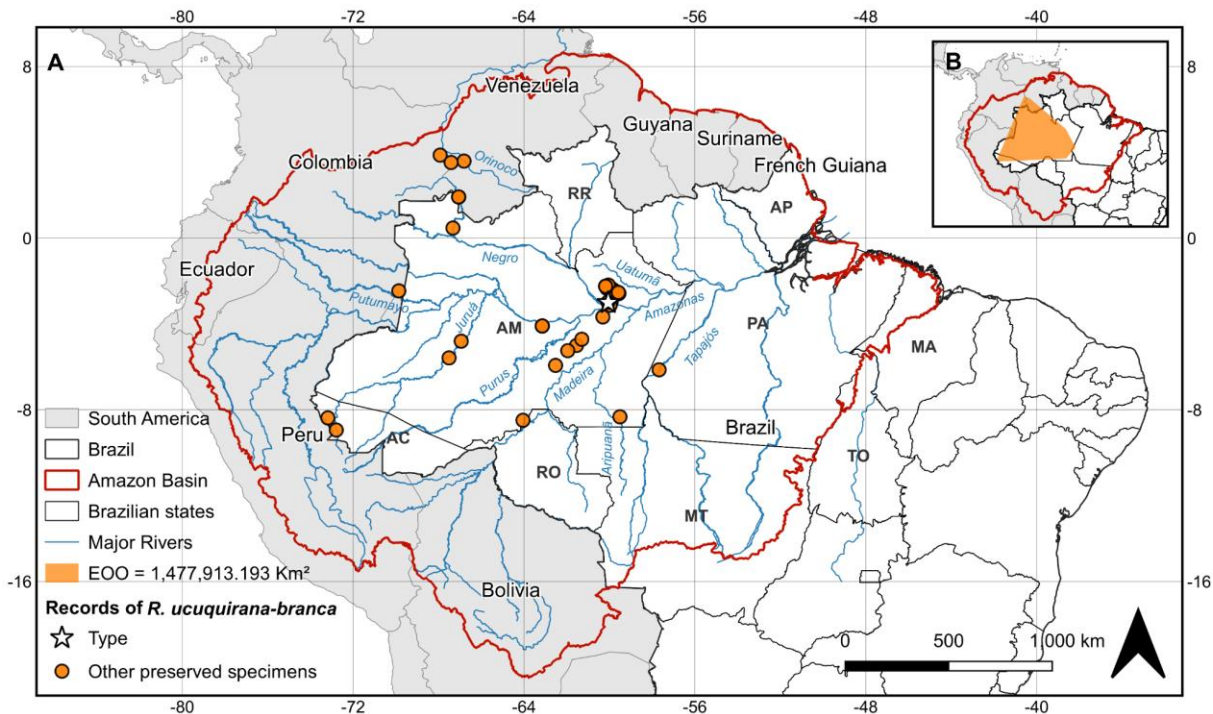


Figure 3. A. Known geographic distribution of *Ragala ucuquirana-branca* (Sapotaceae) across the Amazon Basin; the red outline represents the basin boundary, blue lines represent major rivers, and markers indicate georeferenced records (type represented by a white star and other preserved specimens by orange circles). **B.** Inset map showing the Extent of Occurrence (EOO) of *Ragala ucuquirana-branca* in the study region.

The spatial configuration of the occurrence records defines a broad Extent of Occurrence (EOO) of approximately 1.48 million km², encompassing a substantial portion of the Amazon Basin (Fig. 3B). However, this large EOO contrasts sharply with the sparse and discontinuous distribution of records within it. Occurrences form geographically isolated clusters separated by vast areas without confirmed records, resulting in a fragmented spatial pattern. Even within the EOO polygon, large regions lack occurrences, indicating that the species' distribution is not continuous across its geographic envelope. The Area of Occupancy (AOO) was estimated at 148 km², reflecting the limited number of occupied grid cells within the broader EOO. Together, the EOO and AOO maps highlight the spatial configuration of known records within the Amazon Basin.

Model evaluation revealed consistently high predictive performance across all five algorithms included in the ensemble framework (Table 3). Mean Area Under the Curve (AUC) values were generally high, exceeding 0.80 for most model replicates (Fig. 4A), while True Skill Statistic (TSS) values were predominantly above 0.60 (Fig. 4B), indicating strong discriminatory power between suitable and unsuitable conditions.

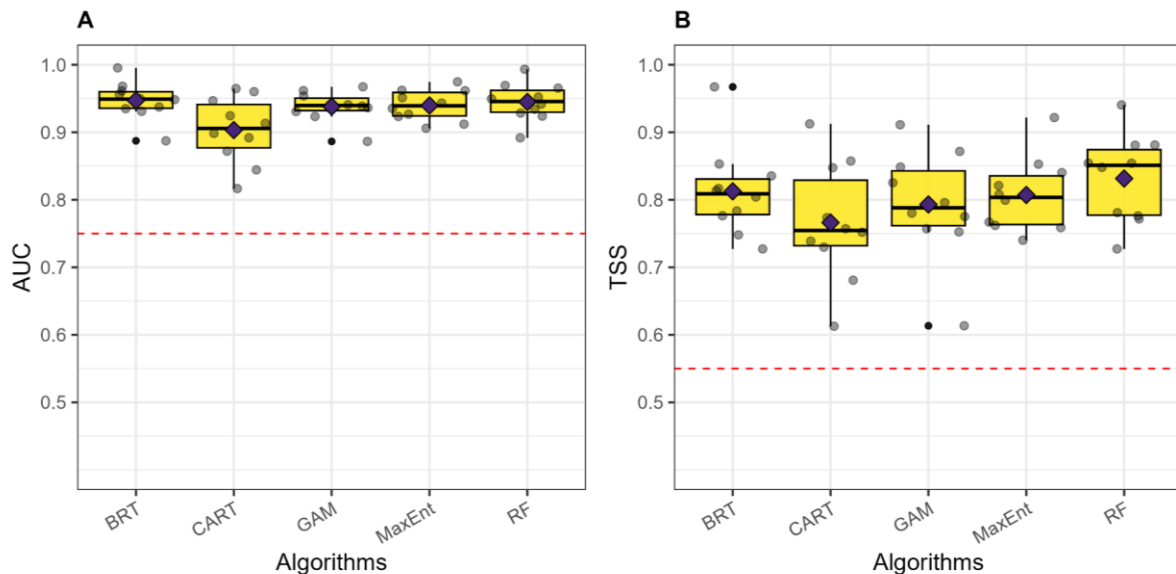


Figure 4. Evaluation of the algorithm performance in the ensemble species distribution model for *Ragala ucuquirana-branca* (Sapotaceae) in the Amazon Basin using (A) AUC and (B) TSS metrics. Each black transparent point represents one model replicate; yellow boxes show the median and interquartile range, and dark purple diamonds mark the mean value for each algorithm. The red dashed line indicates the commonly used threshold for acceptable model performance.

Random Forest (RF) and Boosted Regression Trees (BRT) showed the highest median values for both metrics and the narrowest interquartile ranges, reflecting high stability among replicates. Maximum Entropy also performed robustly, whereas CART and GAM exhibited greater variability, particularly in TSS values, although still meeting minimum performance criteria (Table 3).

Table 3. Mean and standard deviation ($\pm$) of the evaluation metrics for each algorithm in the ensemble species distribution model for *Ragala ucuquirana-branca* (Sapotaceae) in the Amazon Basin.

Algorithm	Area Under the Curve	True Skill Statistic
	Mean $\pm$ SD	Mean $\pm$ SD
Boosted Regression Trees (BRT)	0.95 $\pm$ 0.03	0.81 $\pm$ 0.07
Classification and Regression Trees (CART)	0.90 $\pm$ 0.05	0.77 $\pm$ 0.09
Generalized Additive Model (GAM)	0.94 $\pm$ 0.02	0.79 $\pm$ 0.08
Maximum Entropy (MaxEnt)	0.94 $\pm$ 0.02	0.81 $\pm$ 0.06
Random Forest (RF)	0.95 $\pm$ 0.03	0.83 $\pm$ 0.07

Only model replicates meeting the predefined thresholds ($AUC \geq 0.75$ and $TSS \geq 0.55$) were retained for ensemble construction. This filtering step resulted in a final ensemble characterized by strong internal agreement among algorithms, as indicated by overlapping distributions of performance metrics (Fig. 4). Weighting ensemble predictions by AUC values further reduced the influence of lower-performing models and enhanced the robustness of spatial predictions across the Amazon Basin.

The relative importance of environmental predictors retained in the ensemble model (see Fig. 2 for correlation analysis) shows a markedly uneven pattern (Fig. 5), with a small subset of variables explaining a disproportionate share of the total contribution. Overall, soil-

related predictors accounted for the largest fraction of model importance (44.2%), followed by climate (36.8%), atmosphere (12.1%), land cover (4.5%), and topography (2.4%).

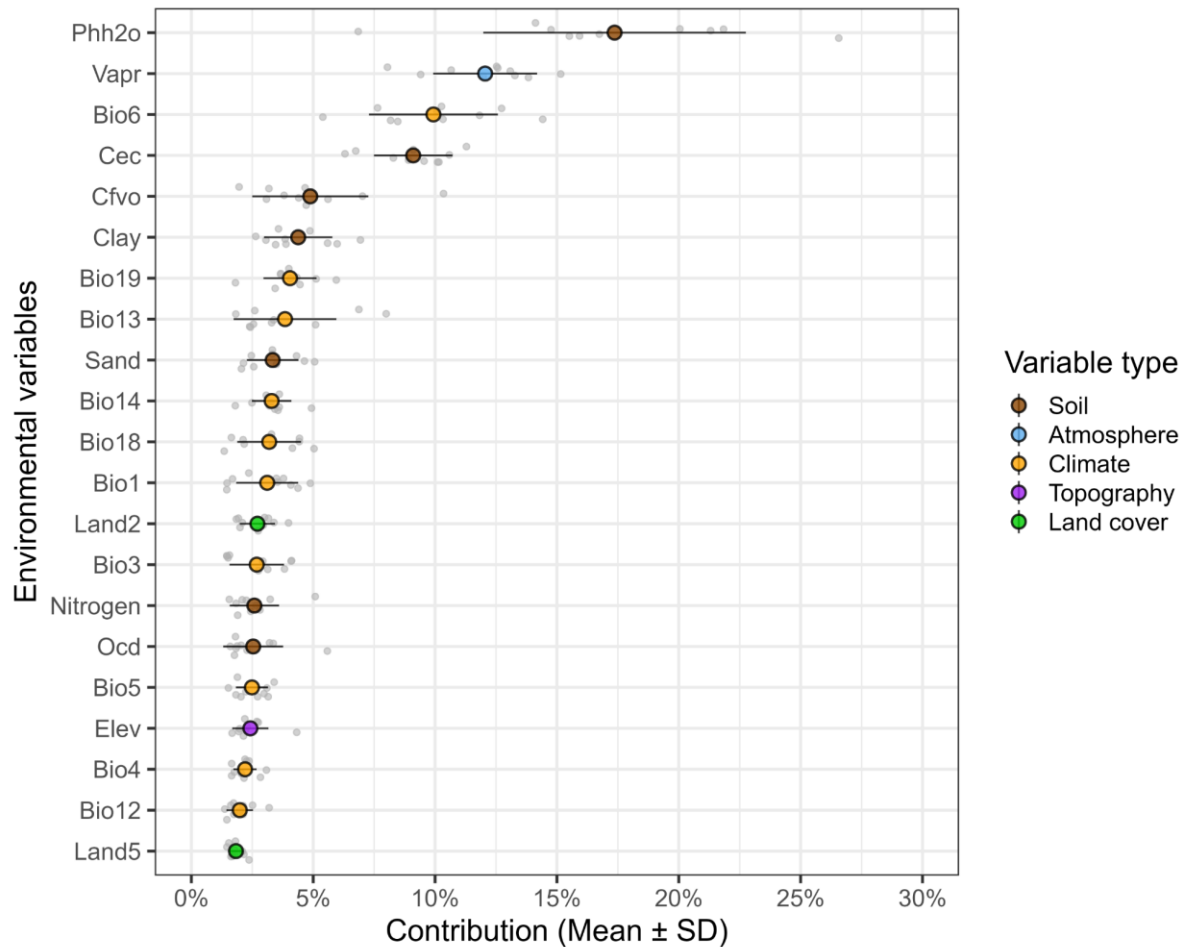


Figure 5. Relative contribution of environmental predictors retained in the ensemble species distribution model for *Ragala ucuquirana-branca* (Sapotaceae) in the Amazon Basin. Predictor importance was weighted by algorithm performance and summarized across model replicates (transparent grey circles). Variables are grouped and color-coded according to environmental category (soil, atmosphere, climate, topography, and land cover). Higher values indicate a greater contribution of each predictor to overall model performance.

Among individual predictors, soil pH measured in water (Phh2o) emerged as the single most influential variable, contributing 17.4% to the ensemble model, and also displaying the highest variability across model runs (SD = 5.4%). This was followed by vapor pressure (Vapr; 12.1%), minimum temperature of the coldest month (Bio6; 9.9%), and cation exchange capacity (Cec; 9.1%). Together, these four predictors accounted for approximately 48.5% of the total explanatory power of the model, indicating that habitat suitability for *R. ucuquirana-branca* is primarily structured along a limited number of key environmental gradients.

Climate variables collectively showed moderate but consistent contributions, with Bio6 standing out as the dominant climatic predictor, while other temperature- and precipitation-related variables (e.g. Bio19, Bio13, Bio14, Bio18) each contributed between ~3–4%. Soil texture and fertility proxies (e.g., clay, sand, Cfvo, nitrogen, and organic carbon density) exhibited intermediate importance values, suggesting a secondary but non-negligible role in shaping suitability patterns. In contrast, land cover variables and topographic elevation

contributed comparatively little to the ensemble model, each individually accounting for less than 3% of total importance.

Overall, the distribution of predictor contributions highlights a strong dependence of the species' modeled distribution on edaphic conditions and atmospheric moisture, modulated by temperature extremes, while broad-scale land cover classes and topography appear to play a minor role at the spatial resolution considered (Fig. 5).

The continuous habitat suitability map derived from the ensemble model revealed a highly heterogeneous and spatially restricted distribution of suitable environments across the Amazon Basin (Fig. 6A). Areas of high suitability (values > 0.9) are not continuous but instead occur as discrete and spatially isolated patches embedded within a largely unsuitable matrix. The most extensive and cohesive suitable areas are concentrated in central Amazonia, whereas smaller and more fragmented patches are predicted in the northwestern and northeastern portions of the basin.

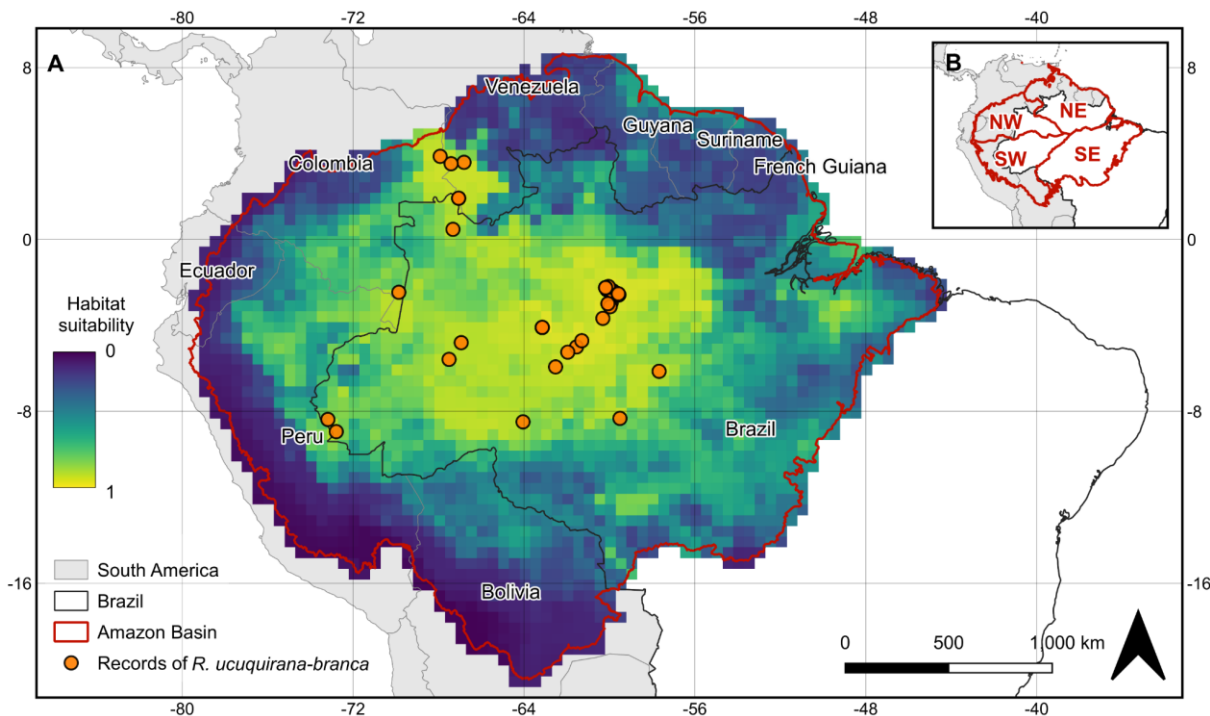


Figure 6. A. Current habitat suitability map derived from an ensemble model using occurrence records of *Ragala ucuquirana-branca* (Sapotaceae) in the Amazon Basin; the red outline represents the Amazon Basin, and the color gradient indicates habitat suitability values, ranging from highly suitable areas (yellow, > 0.9) to extremely unsuitable areas (dark purple, < 0.1). **B.** Inset map showing the geographic subdivisions of the Amazon Basin used for regional interpretation (NW = Northwest, SW = Southwest, NE = Northeast, SE = Southeast).

Despite the species' broad extent of occurrence (EOO), large regions of southwestern and southeastern Amazonia were consistently predicted as having low or negligible suitability. This pronounced mismatch between geographic extent and environmentally suitable area underscores the strong environmental structuring of habitat availability across the basin. Sharp spatial transitions between suitable and unsuitable areas further reflect the high environmental heterogeneity characterizing Amazonian landscapes.

Comparison between continuous suitability predictions and observed occurrence records indicates that most known records fall within areas predicted as moderately to highly suitable, supporting good spatial correspondence between empirical data and model

predictions. At the same time, several areas with high predicted suitability lack confirmed occurrences, suggesting the presence of potentially suitable but undersampled regions within the basin.

Binary projections reinforced the restricted potential occupancy of *Ragala ucuquirana-branca* within the Amazon Basin (Fig. 7). Application of the Minimum Training Presence (MTP) threshold resulted in a relatively inclusive prediction, encompassing all known occurrences and extending into adjacent areas of marginal suitability, particularly in central Amazonia (Fig. 7A).

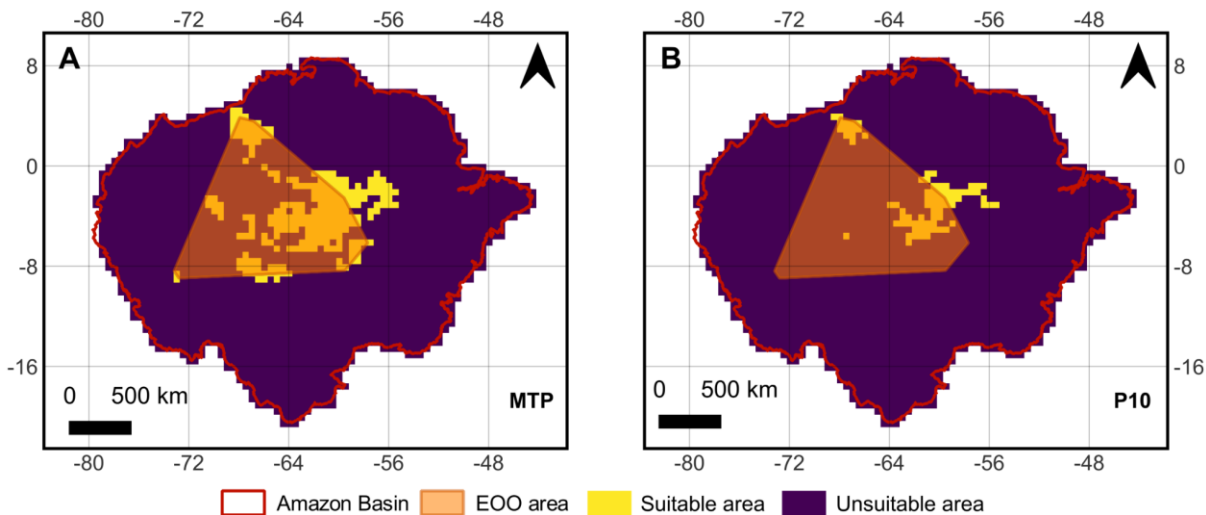


Figure 7. Binary distribution maps of *Ragala ucuquirana-branca* (Sapotaceae) based on two threshold criteria (MTP and P10). **A.** Minimum Training Presence (MTP). **B.** 10th Percentile Training Presence. Yellow areas indicate predicted presence (suitable), and dark purple areas indicate predicted absence (unsuitable) under each threshold criterion. The red outline represents the Amazon Basin, and the orange polygon represents the Extent of Occurrence (EOO).

In contrast, application of the 10th Percentile Training Presence (P10) threshold produced a markedly more conservative projection, restricting suitable habitat to a limited number of core areas characterized by the highest suitability values (Fig. 7B). Under this criterion, large portions of the EOO identified as suitable under the MTP threshold were excluded, and the total area predicted as suitable represented only a small fraction of the Amazon Basin. Notably, both thresholding approaches consistently identified the same core regions, differing primarily in the extent rather than the spatial configuration of suitable areas.

Taken together, occurrence data, variable contributions, continuous suitability maps, and binary projections converge on a consistent empirical pattern: *Ragala ucuquirana-branca* exhibits a broad basin-wide geographic range coupled with environmentally constrained, spatially fragmented, and geographically restricted habitat occupancy.

DISCUSSION

Occurrence data and known geographic distribution

The compiled records from preserved herbarium specimens and long-term forest monitoring plots substantially expand the empirical basis previously available for the species, whose distribution had been documented primarily through sparse records in the last taxonomic

treatments for the genus (e.g., Pennington 1990, 2006). Large portions of the basin that lack confirmed occurrences, including regions that have been historically subject to botanical surveys (Fig. 3A) (Hopkins 2007; Stropp et al. 2020; Carvalho et al. 2023), suggest that the absence of records cannot be attributed solely to sampling gaps. Instead, this pattern points to underlying ecological constraints that limit the establishment of the species across large areas of apparently continuous forest cover.

The pronounced discrepancy between EOO and AOO highlights a strongly aggregated spatial pattern, with occurrences restricted to discrete localities (Gaston 1996; Clavel et al. 2011) rather than being evenly distributed across Amazonian forest cover. This indicates that the species occupies a limited fraction of its overall geographic range.

Taken together, the occurrence data indicate that *R. ucuquirana-branca* is geographically widespread but spatially sparse, with confirmed records forming distinct clusters across the basin. Similar patterns of broad geographic extent combined with highly aggregated occurrence records have been reported for other Amazonian Sapotaceae, including *Ecclinusa guianensis* Eyma (Vasconcelos et al. 2020), *Pradosia ptychandra* (Eyma) T.D.Penn. (Vasconcelos et al. 2024) and *Pouteria decorticans* T.D.Penn. (Gama et al. 2025). This pattern provides an essential empirical baseline for evaluating the environmental drivers and modeled habitat suitability explored in the subsequent sections.

Model performance and ensemble robustness

AUC and TSS metrics indicate a superior predictive capability (Fig. 4), effectively distinguishing between suitable and unsuitable habitats with minimal omission errors (Allouche et al. 2006). The consistently high performance observed across algorithms is in agreement with previous studies showing that machine learning methods are more adept at capturing complex, non-linear interactions between abiotic variables and species presence than traditional frequentist models (Elith et al. 2008; Elith and Leathwick 2009).

The strength of the ensemble approach lies in its ability to mitigate the individual biases of different algorithms, providing a consensus projection that is generally more robust and biologically realistic than single-model outputs (Araújo and New 2007; Marmion et al. 2009). By combining predictions across algorithms, ensemble models tend to reduce overfitting commonly observed in high-performance methods such as MaxEnt or Random Forest, resulting in more conservative and reliable suitability estimates. This methodological rigor increases confidence that the identified suitability hotspots are not merely artifacts of sampling bias but instead reflect areas where the environmental conditions fall within the core ecological envelope of *Ragala ucuquirana-branca* (Phillips et al. 2009).

Environmental drivers of distribution

In the Amazon, soil chemistry acts as a powerful filter; species adapted to specific pH levels are often associated with physiological trade-offs that prevent them from competing in soils with different nutrient availabilities or aluminum toxicity levels (Phillips et al. 2003; John et al. 2007; Quesada et al. 2012; Condit et al. 2013; Figueiredo et al. 2018).

Furthermore, the influence of vapor pressure and Bio6 suggests a narrow physiological tolerance for atmospheric water demand and thermal stress. Vapor pressure, closely related to atmospheric water demand and vapor pressure deficit, influences stomatal regulation in canopy trees, limiting carbon assimilation and growth (Esquivel-Muelbert et al. 2017; Grossiord et al. 2020). The reliance on stable, humid conditions explains the species' absence from the more seasonal fringes of the southern and eastern Amazon. This suggests that the species' distribution is governed by a dual-filter system: a chemical filter at the

rhizosphere (pH) (e.g., Dubuis et al. 2013) and a physical filter at the leaf-atmosphere interface (Vapor pressure) (e.g., Salm et al. 2007), both of which must be met simultaneously for the species to persist.

Cec is a useful indicator of soil fertility because it reflects the soil's ability to retain and exchange essential nutrients and is closely associated with clay mineralogy and organic matter content. Its relevance suggests that *R. ucuquirana-branca* may preferentially occur in soils with greater nutrient-retention capacity, which can buffer nutrient limitation in highly weathered Amazonian substrates. Similar associations between Cec and tree species distributions have been documented for several Amazonian forest communities (Phillips et al. 2003; Quesada et al. 2012; Toledo et al. 2017). Together, these results indicate that the realized niche of *R. ucuquirana-branca* is shaped by a tight coupling between belowground chemical constraints and aboveground atmospheric conditions, reinforcing the view that multiple, interacting environmental filters determine tree species distributions in the Amazon.

Predicted habitat suitability across the Amazon Basin

The fact that the ensemble model predicts low suitability in regions with different soil pH and atmospheric moisture, even those historically subject to botanical surveys, strongly supports the hypothesis of edaphic specialization over a simple sampling artifact. This suggests that *R. ucuquirana-branca* is a true habitat specialist whose occupancy is physically constrained by the weathered substrates and stable climates of the central-western core.

The concentration of highly suitable areas in the central-western Amazonia suggests the existence of a core ecological region for the species, where environmental conditions closely match its physiological and edaphic requirements. In contrast, marginal areas toward the eastern and southern basin likely represent environments beyond the species' tolerance limits, rather than zones of transient occupancy. The isolated "islands" of habitat (Fig. 7) suggest that much of the eastern basin is environmentally marginal or entirely unsuitable, likely due to the combined effects of lower soil fertility and increased climatic seasonality (Toledo et al. 2017).

This projected fragmentation has deep evolutionary and ecological implications. Small, isolated patches of suitable habitat can lead to reduced gene flow and increased vulnerability to stochastic events (Rosas et al. 2011). As climate change alters rainfall patterns and vapor pressure across the basin (Esquivel-Muelbert et al. 2019; Flores et al. 2024; Lima et al. 2026), these core areas may shrink further under projected increases in climatic seasonality and atmospheric water demand. The suitability gap observed in the southern Amazonia acts as a contemporary barrier, suggesting that the species may be unable to migrate southward in response to changing climates, effectively trapping populations in the central basin (Araújo and Pearson 2005; Bush et al. 2011).

Taxonomic and ecological implications

Our results indicate that *Ragala ucuquirana-branca* is characterized by ecological specialization associated with soil chemical properties and atmospheric stability, rather than broad environmental tolerance. This finding has important implications for taxonomy, as environmentally structured distributions may contribute to morphological and genetic differentiation across the species' range, a pattern frequently observed in Amazonian lineages (Gentry 1981; Tuomisto et al. 2003; Fine et al. 2005, 2014). The environmentally structured distribution revealed by the SDM provides testable hypotheses for future taxonomic and phylogeographic studies. If populations occupying distinct soil or climatic domains exhibit

consistent morphological or genetic differentiation, this would support the role of ecological specialization as a driver of diversification within the lineage.

From a conservation standpoint, the restricted AOO and the concentration of highly suitable habitats in environmentally stable regions highlight potential vulnerability to ongoing climatic change and land-use intensification, particularly in southeastern Amazonia. Integrating SDM outputs with field-based inventories and phylogeographic data will be essential for refining conservation assessments and understanding the evolutionary and ecological processes shaping the distribution of *R. ucuquirana-branca*.

CONCLUSIONS

Our study provides the first assessment of the environmental drivers and potential distribution of *Ragala ucuquirana-branca* across the Amazon Basin, illustrating how edaphic and atmospheric filters can decouple geographic range size from effective habitat occupancy in Amazonian trees. Our results demonstrate that the species' distribution is not determined solely by broad climatic gradients, but is strongly filtered by specific edaphic conditions, particularly soil pH, in combination with atmospheric moisture stability.

The high predictive performance of the ensemble model supports the identification of the western and central Amazonia as the main biophysical strongholds for the species. The marked discrepancy between the large Extent of Occurrence (EOO) and the highly restricted Area of Occupancy (AOO) highlights pronounced ecological specialization and potential vulnerability, consistent with a narrow niche breadth and limited tolerance to environmental heterogeneity. As an edaphic specialist, *R. ucuquirana-branca* occupies fragmented and environmentally stable habitats, which may increasingly constrain gene flow and long-term resilience under ongoing environmental change.

From a conservation perspective, the species' dependence on specific soil chemistry and stable atmospheric moisture regimes makes it particularly sensitive to the combined effects of deforestation and climate change. More broadly, our findings emphasize the need to move beyond climate-only frameworks when assessing species rarity, vulnerability, and conservation priorities in hyperdiverse tropical forests.

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